

Chapter 23

Functional Diversity in Plants: Implications for Conservation Issues of the Mexican Biodiversity



Clara Tinoco-Ojanguren, José L. Andrade, Oscar Briones,
and Alejandro E. Castellanos

Abstract In this chapter, we explore the functional diversity concept and its importance in several ecological issues, especially maintenance of ecosystem services and conservation. We consider that Mexico's species megadiversity should be reflected into a high functional diversity. However, our knowledge on this issue is still limited. Interest in the functional diversity approach has just increased in Mexico. Despite that, since the 1970s, ecophysiological research in Mexican ecosystems has had important pioneer contributions to our knowledge on functional traits in plants and its ecological importance. In this chapter, we review some case studies describing our knowledge of plant physiological diversity in different ecosystems, as examples of the high functional diversity in Mexico. Unfortunately anthropogenic disturbance is increasingly affecting species biodiversity, in particular the more vulnerable species and ecosystems. Increasing research on the functional traits of Mexican ecosystems will provide important information about species function at the ecosystem level and species vulnerability in the context of human disturbance and/or climatic change. Studies focused in functional diversity as an important component of biodiversity will provide us a solid base for planning on conservation decisions, restoration programs, and maintenance of ecosystem services.

C. Tinoco-Ojanguren (✉)

Ecología de la biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, Hermosillo, Sonora, Mexico

e-mail: claral@unam.mx

J. L. Andrade

Centro de Investigación Científica de Yucatán, A. C, Unidad de Recursos Naturales, Mérida, Yucatán, Mexico

e-mail: andrade@cicy.mx

O. Briones

Instituto de Ecología, A.C, Veracruz, Mexico

e-mail: oscar.briones@inecol.mx

A. E. Castellanos

DICTUS, Universidad de Sonora, Hermosillo, Sonora, Mexico

e-mail: alejandro.castellanos@unison.mx

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23.1 Functional Diversity: Concept and Importance

Biodiversity is a multidimensional concept defining the variability of living beings, their functions and ecological complexes. It includes four components: species diversity, genetic diversity, ecological diversity, and functional or physiological diversity. Until recently functional diversity (FD) has been considered an important component of biodiversity. Diaz et al. (2007) define functional diversity as the type, range, and relative abundance of functional traits in a community. Functional traits are morphological, physiological, and phenological traits of individuals that influence growth, reproduction, and survivorship and therefore have an effect on fitness (Violle et al. 2007; Orozco-Segovia and Sanchez-Coronado 2009). Knowledge on functional traits is important to understand the mechanistic basis of species distribution, their response to environmental changes, their biotic interactions, and their role in ecosystem processes. For example, the relative abundance and diversity of species attributes in response to environmental gradients, biogeographic regions, or human disturbance, such as cattle grazing, change the functional diversity of ecosystems (Diaz et al. 2003, 2007). At a higher scale (communities), FD is the key to define the mechanisms that link biodiversity and ecosystems function (Diaz 2001 for a review; Cadotte et al. 2011).

As a growing and complex research area, there is not a unique methodology to measure FD. Most knowledge on FD has been generated at the individual and population levels since the 1970s, when technological advances allowed the possibility for ecophysiological studies. From these studies, common and meaningful traits have been collected and analyzed. To date, there are standardized protocols to measure some functional traits that are frequently measured in ecophysiological studies (Cornelisen et al. 2003). However, the selection of the system and meaningful traits to be measured depend on the study question; it is also important to include several traits to decrease the probability of species redundancy and to measure quantitative traits to capture interspecific variability (Orlandi Laureto et al. 2015). Estimations of functional diversity at more complex levels (communities) is not an easy task; therefore, indexes and models have been proposed as an approach to calculate FD (Carmona et al. 2018; Pakeman 2011).

Mexico is one of the megadiverse countries of the world; it harbors 12% of the world biodiversity, despite being a relatively small country, with 1.4% of the planet land surface. Its biological diversity is associated with the following factors: high variety of climates, complex geological history, topographic heterogeneity, and a geographical location in a wide range of latitude ($14^{\circ} 32' 27''$ – $32^{\circ} 43' 06''$ N), resulting in a mosaic of environmental conditions. Environmental heterogeneity has led to a great variety of habitats where a high number of organisms have evolved and coexist. Furthermore, Mexico is the site of confluence of the Nearctic and Neotropical biogeographic regions, where boreal and tropical organisms converge,

increasing biodiversity of species and ecosystems. Under this scenario, it is not hard to think that Mexican biodiversity is associated with a high functional diversity that might evolve in response to this highly heterogeneous environment.

Although we require more research to be focused on functional diversity to build a good scientific basis to preserve Mexico's biodiversity, conservation measurements should be a priority. In this chapter, we include some case studies describing our knowledge on plant physiological diversity for different ecosystems, as a sample of the high functional diversity in Mexico.

23.2 Functional Diversity in Seasonally Dry Forest: Plants with Crassulacean Acid Metabolism

23.2.1 Plants with Crassulacean Acid Metabolism in Seasonally Dry Forests

Crassulacean acid metabolism (CAM) is an adaptation for some plants to concentrate atmospheric carbon dioxide (CO₂) within their cells (Winter and Smith 1996; Lüttge 2004; Andrade et al. 2007). CAM is common in plants living in environments with long periods without water but also exists in aquatic plants that inhabit places where CO₂ becomes scarce during the day (Keeley and Rundel 2003). Nonaquatic CAM species assimilate CO₂ when air temperature is lower and relative humidity is higher, which is generally at night; this allows less water loss by transpiration and permits high water use efficiency. CAM plants have greater water use efficiency than C₃ and C₄ plants under similar conditions; therefore, they are distinctive of arid and semiarid regions and of forest canopies (Drennan and Nobel 2000; Winter et al. 2005; Andrade et al. 2009). In Mexico, CAM plants are emblematic, revealed in many cultural aspects, and they have even gone beyond borders: *Opuntia* spp. are the most extensively cultivated CAM crop worldwide, exceeding that of the better known pineapple (Nobel 2002; de la Barrera and Andrade 2005).

Mexican CAM plants inhabit in virtually all terrestrial ecosystems below 2000 m asl (Körner et al. 1991; Vargas-Soto et al. 2009), but the great aridity of the Mexican territory significantly favors them. In fact, Mexico is the center of origin and diversification of cacti and other CAM species, and, because most of these species are endemic, they are particularly vulnerable to changes in land use. In tropical areas, CAM species are terrestrial in short-statured communities such as dunes and dry deciduous forests and predominantly epiphytes or hemiepiphytes in taller forests (Ricalde et al. 2010; Valdez-Hernández et al. 2015). In fact, epiphytic CAM species probably also outnumber terrestrial CAM species in Mexico (Andrade et al. 2007; Silvera and Lasso 2016; Zotz 2016). In seasonally dry forests, where dry season can last several weeks, CAM species comprise important functional groups, which can be source of water and food for animals during drought; this is because they have leaves or stems structurally transformed to store or trap water (Martínez-Ramos 2008).

At a global scale, tropical seasonally dry forests are the less understood and represent one of the most threatened ecosystems (Miles et al. 2006). In Mexico, they are also the less protected even with their floristic richness and endemism (Trejo and Dirzo 2002; Dick and Wright 2005). This type of vegetation is characterized, depending of the precipitation, by having 25–100% of the composing tree species losing their leaves during the dry season (Miranda and Hernández 1963), when light intensity and air temperatures can change dramatically (Graham and Andrade 2004). Dry deciduous forests of Mexico are rich in CAM species, which are from diverse families and at high densities, and in some forests, some terrestrial species can even be ecologically the most important species (Ricalde et al. 2010). Moreover, abundance of nitrogen fixer legumes in some dry forests can induce growth in accompanying terrestrial CAM plants since epiphytic CAM species receive most of their nitrogen from atmospheric sources (Santiago et al. 2017). Additionally, relative capacitance (the capacity of the tissues to maintain their water potentials when the water content decreases) is higher for terrestrial CAM species than for CAM epiphytes (Andrade et al. 2009).

23.2.2 *Terrestrial CAM Species*

Terrestrial CAM plants have succulent stems or leaves that store water. Also, rosette forms of species from several CAM families have a role to capture rainfall and even fog (Martorell and Ezcurra 2002). So, these specialized storage tissues can transport water to maintain turgor in the photosynthetic tissues during drought (Goldstein et al. 1991; Lüttge 2004; Andrade et al. 2009). In the rainy season, CAM photosynthesis can enhance; many studies reveal that the greatest tissue acid accumulation (a proxy for CO₂ uptake) of terrestrial CAM plants in seasonally dry forests takes place during the rainy season (Andrade et al. 2006; Cervera et al. 2007; Vargas-Soto et al. 2009; González-Salvatierra et al. 2010; Ricalde et al. 2010), with lower air temperatures and vapor pressure deficits than during the rest of the year.

Seedlings of terrestrial CAM plants cannot have enough water in their tissues to endure long dry seasons but have higher survival probabilities under the canopy of nurse plants (Esparza-Olguín et al. 2002; Flores et al. 2004; Cervera et al. 2006). Although this phenomenon has been widely documented in different sites (Valiente-Banuet and Ezcurra 1991; Godínez-Álvarez et al. 1999, 2003), few studies have measured microenvironmental and physiological differences for seedlings and adults, which provide information for conservation purposes. For instance, seedlings of the rare cactus *Mammillaria gaumeri* do not survive under more than 20% of ambient light; however, adults increase growth at exposed locations (40–80% of ambient light), indicating that some disturbances can be beneficial for adults of this species (Cervera et al. 2006, 2007).

The enzyme that fixes CO₂ at night in CAM plants, phosphoenolpyruvate carboxylase (PEPc), does not discriminate against ¹³CO₂, whereas ribulose biphosphate carboxylase (RuBisCO), which fixes carbon during the day, favors ¹²C fixation.

Then, studies on carbon isotopic composition ($\delta^{13}\text{C}$) provide information on the proportion of CO_2 fixed during the night or day (Griffiths 1992). CAM plants with CO_2 uptake exclusively at night, by PEPc, would have $\delta^{13}\text{C}$ values around -11‰ (close to atmospheric values), whereas if all CO_2 is fixed by RuBisCO the values of $\delta^{13}\text{C}$ would be about -27‰ (O'Leary 1988). In northern Yucatan, tissue $\delta^{13}\text{C}$ values for terrestrial CAM plants of the coastal dunes are 2‰ higher than CAM plants from the tropical dry deciduous forests (Ricalde et al. 2010), which indicates greater CO_2 fixation through the CAM pathway in sites with less water.

During the dry season, the lack of water and high temperatures can affect growth and reproduction of CAM species; high temperatures increase respiratory rates, and plant tissues must invest photosynthetic products to repair the photosynthetic apparatus from photoinhibitory damage, which leads to lower investment against pathogens and predators (Cervantes et al. 2005; Andrade et al. 2009). Optimal diurnal/nocturnal temperature for CO_2 uptake of some species in seasonal dry forests is 30/20 °C (Nobel 1985; Nobel and de la Barrera 2002). Temperatures above or below this optimal, especially the nocturnal ones, reduce growth in CAM plants (Andrade et al. 2007).

A specific group of terrestrial CAM plants belongs to the genus *Clusia*, with species with C_3 , C_3/CAM , and CAM pathways (Winter and Smith 1996; Winter et al. 2005; Lüttge 2006). In Mexico, there is a preponderance of C_3/CAM *Clusia* species, but in seasonally dry forests, all species are CAM (Vargas-Soto et al. 2009).

23.2.3 Epiphytic CAM

Vascular epiphytes inhabit a very dynamic microenvironment, where light, nutrients, and water can change drastically in time and space (Benzing 1990; Lüttge 2008; Zotz 2016). In seasonal dry forests, epiphytes are prevalently CAM, but they have also evolved several morphophysiological adaptations such as succulence, reduced stomatal size and density, and specialized root, leaf, and stem structures (Winter et al. 2005; Andrade et al. 2009; Petter et al. 2015; Zotz 2016). Epiphytes from seasonally dry forests of Mexico also represent a main group of interest for physiological studies even though they are not as diverse, abundant, or important in biomass as in wet forests.

Vertical distribution of epiphytes in the dry forests is more related to light than to host tree species; most species are concentrated in the middle part of the host trees, mainly on the main stem or in branches near the main stem (Cervantes et al. 2005; Reyes-García et al. 2008; Cach-Pérez et al. 2013; Chilpa-Galván et al. 2013; de la Rosa-Manzano et al. 2014a). Some studies suggest that species distributed within the lower canopy avoid excess radiation (Griffiths and Maxwell 1999; Reyes-García and Griffiths 2009; Reyes-García et al. 2012). Indeed, species within the upper canopy can be more tolerant to high light but paradoxically may also be able to obtain more water (rainfall, fog, and dew) than species in the lower canopy (Andrade 2003;

Graham and Andrade 2004; Reyes-García et al. 2012). However, although microclimatic conditions can contribute to the vertical distribution of CAM epiphytes in tropical dry forests, factors such as seed dispersers, bark traits, competition, facilitation, and other variables need further investigation to determine their role on such distribution (Benzing 1990; Chilpa-Galván et al. 2017).

Additionally, epiphytes with CAM have a morphology and physiology modified to tolerate water scarcity and high light incidence (Benzing 1990; Zotz and Hietz 2001). For instance, epiphytic bromeliads may store water in succulent tissues or in water-storing tanks and may absorb water and nutrients through modified leaf trichomes (Benzing 1990; Reyes-García et al. 2012). Epiphytic orchids have water storage capacity in their stems or pseudobulbs and on specialized roots with a highly absorptive velamen (de la Rosa et al. 2014b). Also, epiphytic bromeliad densities are inversely related to vapor pressure deficit (VPD, Cach-Pérez et al. 2013). Low values of VPD diminish the rate of water loss and allow a high probability for deposition of dew (Chilpa-Galván et al. 2013; de la Rosa et al. 2014b). In the north of Yucatan, water table can be very shallow, and, in locations where trees can reach it, low-VPD canopy islands emerge with high epiphyte densities (Chilpa-Galván et al. 2013).

In seasonally dry forests, the open canopy of trees and pinnate leaves offer poor protection to epiphytes against high incident light. Furthermore, trees also lose their leaves during the dry season with a consequent increase in photooxidative stress in epiphytic leaves, which carries a decrease in the quantum efficiency of photosystem II and a decline in CO₂ assimilation (Valdez-Hernández et al. 2015). However, it has been reported that epiphytes with CAM avoid the production of the harmful reactive oxygen species, reducing photoinhibition and oxidative stress (Niewiadomska and Borland 2008). CAM is advantageous to cope with drought because it creates high CO₂ concentrations in the cytosol and chloroplasts, favoring Rubisco's carboxylation activity over its oxygenase activity, maintaining electron transport, and preventing damage to photosystems (Niewiadomska and Borland 2008). Moreover, epiphytic bromeliads increased the production of antioxidant compounds and flavonoids as a response to high light and other stressful conditions (Saito and Harborne 1983; González-Salvatierra et al. 2010). Also, leaf trichomes on bromeliads are highly reflective and could have an important role in photoprotection of leaves exposed to direct sunlight (Pierce 2007). For instance, individuals of tank species on deciduous hosts in short-statured dry forests have larger trichomes compared to species on host in taller less drier forests (Cach-Pérez et al. 2016).

Epiphytic orchids have also diverse mechanisms to remove or avoid excess light and heat, including a reduction of leaf area to increase heat flux by conduction and convection, carotenoid production, and photosystem II heat dissipation of absorbed energy (Vaz et al. 2004; Adams et al. 2008; de la Rosa-Manzano et al. 2014b, 2015). Not surprisingly, epiphytic orchids produce more carotenoids (such as lutein and neoxanthin) during the dry season than during the wet and early dry seasons in tropical dry forests; also, the concentrations of these

pigment are higher in leaves of orchids from the deciduous forest than those from the semi-deciduous forest (de la Rosa-Manzano et al. 2015). These differences in carotenoid compositions between epiphytic plants growing at high vs. low light are similar to the general plant responses reported by Demmig-Adams and Adams (1992).

Additionally, orchid leaves from a dry deciduous forest have higher zeaxanthin retention and lower values of maximum quantum efficiency of photosystem II (F_v/F_m) during the dry season than orchids from a semi-deciduous forest (de la Rosa-Manzano et al. 2015). These changes are related to high incident light and the prolonged dry period that occur in the tropical dry deciduous forests, when practically all trees shed their leaves. Moreover, in contrast to terrestrial CAM species, for epiphytes CAM photosynthesis enhances during the early dry season, particularly in the dry deciduous forest, when lower air temperatures, light, and minimal VPD occur than during the rest of the year (de la Rosa-Manzano et al. 2014b, 2015); indeed, dew and fog have higher deposition rates during this season (Andrade 2003; Reyes-García et al. 2012), which are conditions that favored a higher stomatal conductance to increase CO_2 uptake.

Epiphytes have a distinct isotopic composition of nitrogen (^{15}N) values in a tropical dry deciduous forest because they must obtain most of their N from the atmospheric sources than for decaying organic matter (Santiago et al. 2017). Low ^{15}N values in epiphytes have been reported for other forests and for organic N in precipitation of non-polluted areas (Stewart et al. 1995; Cornell et al. 1995; Hietz et al. 1999).

It would be important to study multiple stress factors for CAM epiphytes in combination to measure plasticity and predict plant responses to future climate change (Prasch and Sonnewald 2015; de la Rosa-Manzano et al. 2017), vital information for conservation, and restoration programs. Since the future of epiphytes is uncertain in this changing world (Zotz 2016), research that highlights the potential of these species as ornamentals or biological indicators is extremely important.

23.3 Functional Diversity in Drylands: Environmental Tolerance and Species Adaptation in Mexican Drylands

Diversity and abundance of response traits change in plant communities in response to historical, biogeographical, and environmental local effects and more recently to man-made disturbances and global change. Functional diversity in plant communities of dryland ecosystems reflects the different adaptive responses to water limitations. Low and infrequent precipitation amounts and rainfall events or pulses with extreme high temperatures are the main selective factors for the different functional groups in dryland ecosystems (Noy-Meir 1973; Schwinning and Ehleringer 2001; Reynolds et al. 2004). In Mexican drylands, plant functional groups are numerous

considering the different adaptive responses of leaves, stems, and roots to selective environmental and biological factors (Shreve 1942; Miranda and Hernández-Xolocotzi 1963). Response traits have an effect and influence ecosystem function as species ecophysiological traits are affected by the environment. For example, functional diversity in Mexican dryland species correlate with morpho-structural proxies of drought-enduring mechanisms such as leaf and leaflet size and life span, stem height and numbers, and root and water storage characteristics (Miranda and Hernández-Xolocotzi 1963) that are a consequence of the diverse adaptive ecophysiological responses, such as temperature and drought tolerances, photosynthetic capability, and water use efficiency (Flexas et al. 2002; Castellanos et al. 2010; Ryel et al. 2010; Medrano et al. 2015).

Mexican drylands are widespread and cover about 55–60% of the country, most of which correspond to the Northern Chihuahuan and Sonoran deserts. In Northwestern Mexico in the Sonoran Desert, the Neotropical and Temperate biogeographic regions meet in the Central Region of Sonora (Rzedowski 1978; Castellanos et al. 2010) and sustain some of the largest diversity of plant functional types. An example of the functional diversity in that region is the presence of one of the most abundant vine floras in the world (Castellanos 1991; Rundel and Franklin 1991; Molina-Freaner et al. 2004), even though vine species diversity are known to decrease from the tropics to temperate regions (Gentry 1983; Ewers et al. 1991). Vine species are present in the region and their diversity increase toward the high rainfall end of a precipitation gradient. Measured for C_3 species only, mean vines species increase their water use efficiency in the driest sites, but their mean water use efficiency was lower in sites with higher annual rainfall, as measured by isotopic ^{13}C discrimination (Table 23.1). Differential leaf isotopic carbon discrimination by the photosynthetic enzyme RUBISCO (ribulose biphosphate carboxylase-oxygenase) and stomatal control is correlated to water use efficiency and reflect the different long-term physiological mechanisms that control water loss, such as smaller diameter in xylem cells and hydraulic conductivity and stomatal regulation to minimize leaf transpiration under the region harsh environments (Castellanos 1991; Molina-Freaner and Tinoco-Ojanguren 1997; Castellanos et al. 1999; Molina-Freaner et al. 2004). As in other studies, we found larger variability in the functional diversity within site than between sites.

Drylands species have a number of other different functional strategies and attributes that allow them to adapt to the limiting water conditions of dryland

Table 23.1 Overall mean ^{13}C isotopic ratio for species in each of five sites along an aridity gradient in Sonora in Northwestern Mexico

Sites	Rainfall (mm)	$\delta^{13}C$	s.e.	
BK	121.8	26.74	0.09	<i>a</i>
HMO	349.3	27.51	0.12	<i>ab</i>
COL	348.9	28.32	0.19	<i>cd</i>
SFO	431.1	28.04	0.13	<i>bc</i>
SJV	524.2	28.99	0.16	<i>d</i>
Mean		28.33	0.09	

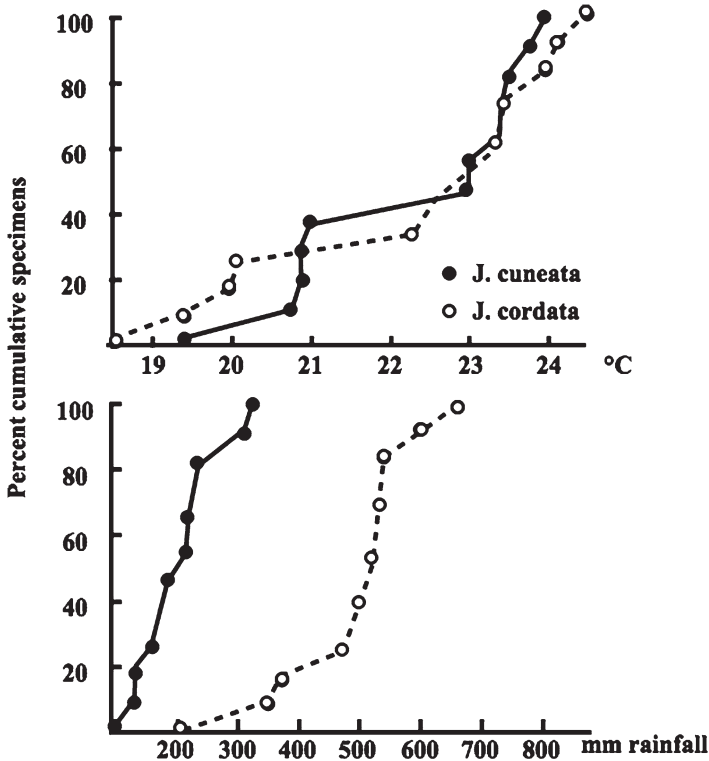


Fig. 23.1 Percent cumulative number of specimens of *Jatropha* species versus their mean annual temperature and rainfall along their known range of geographic distribution. Data were obtained with MaxEnt tool for species distribution modeling

habitats, such as the increasing niche differentiation within their biogeographic distribution range. *Jatropha* species are able to differentiate their species distribution ranges, within the arid and subtropical ecosystems in Northwestern Mexico, along both precipitation and temperature gradients (Fig. 23.1). *J. cuneata*, a species characteristic of some of the most arid regions of Mexico, has a lower and much narrower range of precipitation in their habitats. On the contrary, *J. cordata*, a characteristic species to subtropical shrublands and deciduous forests in Northwestern Mexico (INEGI 2000), has a wider range of precipitation in the habitats it is found. Both *Jatropha* species are drought evaders, and their fleshy roots and stems may store important amounts of water, such that when water is available, they sustain some of the highest leaf water potentials during the day, compared to other species in the same site (Table 23.2). Poor stomatal control of *Jatropha* leaves, however, may be responsible for their rapid leaf senescence, soon at the end of the rainfall season (Castellanos pers. obs.). *Jatropha* also characterize the contribution of species from the subtropical biogeographic regions to the large diversity and contrasting physiological responses and adaptations of plant functional types in the drylands of Mexico.

Table 23.2 Predawn water potentials for different functional-type species from the Sonoran Desert in Mexico

Species	Growth form	Predawn water potential (-MPa)	Root depth (cm)
<i>Olneya tesota</i>	Evergreen tree	3.85	145–180
<i>Jatropha cordata</i>	Succulent deciduous tree	0.72	45–60*
<i>Mimosa laxiflora</i>	Shrub	6.00	145
<i>Jatropha cardiophylla</i>	Succulent shrub	0.25	60–90*
<i>Encelia farinosa</i>	Perennial herb	3.10	15–50

Rooting depth assumes night equilibrium of plant and soil water potentials and with roots in *Jatropha* species

23.3.1 Threatens to Functional Diversity in Mexican Drylands: Global Change and Land Use Cover Change

The large contribution of Neotropical floristic elements to the functional diversity of Mexican drylands may also be the major drawback to their richness and functional diversity in the future. Given the current scenarios and the major drivers of global change, increasing atmospheric CO₂ concentration, GH gases, and land use changes and deforestation, their effects are more notorious in Mexican drylands. Global change will increase annual temperatures, decrease rainfall amount, and change their seasonality (Seager et al. 2007b, 2009). Global change will have unknown but likely differentiated effects on species niche distribution (Villaseñor and Téllez-Valdés 2004; Moghaddam-Gheshlagh et al. 2017); their abundance, composition, and diversity (Archer et al. 1995; Archer and Predick 2008); biogeochemical cycles (Delgado-Baquerizo et al. 2013; Yuan and Chen 2015); and ecosystem function (Smith et al. 1997; Pan 2000; Chapin 2003). In the Central Region of Sonora, for example, *Jatropha* species, *J. cuneata* and *J. cordata*, have easily differentiated distribution niches along a rainfall, but not a temperature gradient (Fig. 23.1). Given the proposed global change scenarios of increasing temperature and decreasing rainfall in the region (Seager et al. 2007a, b), it is expected that *J. cuneata* will expand their range of distribution, and *J. cordata* will be the most affected, decreasing their distribution and abundance in the future, as current populations are commonly found in habitats with 350 mm annual precipitation or more. It is clear that many more ecophysiological studies are needed to determine the extent and severity of local effects of global change in the different plant species in Mexican drylands.

Change in arid land use is the main driver of global change in Mexican drylands. For more than 400 years, cattle grazing has been a major activity in arid plant communities and have induced changes in species abundance and composition, reducing the most palatable and increasing the more unpalatable (McIntyre et al. 2003; Callaway et al. 2005; Díaz et al. 2007; Dorrrough et al. 2007; Hanke et al. 2014). In some drylands plant communities, overgrazing was detected, probably accentuated

by a period of prolonged droughts, during the 1850s (Archer et al. 1995; Buffington and Herbel 1965; Seager et al. 2007a). During the mid-1950s, introduction of exotic grasses and rotation of grazing lands increased cattle stocking level in ranches (Bravo-Peña et al. 2010; Castellanos et al. 2010; Brenner 2011). Some of the ecological and environmental consequences of those management practices are still unknown and unmeasured.

Functional diversity is reduced after exotic buffelgrass savannas are established. Bulldozing of plant communities to establish buffelgrass grasslands or savannas removes most of herbs, shrubs, and most species of trees, reducing plant diversity (Saucedo-Monarque et al. 1997; Castellanos et al. 2002). Once buffelgrass is established, there may be some reestablishment of trees and shrubs (Castellanos et al. 2010; Tinoco-Ojanguren et al. 2013), although some others may be inhibited (Morales-Romero and Molina-Freaner 2008; Morales-Romero et al. 2012). In sites where buffelgrass savannas were established, many other functional processes may be changed. We have documented changes in ecosystem productivity (Hinojo-Hinojo et al. 2016), nitrogen mineralization (Celaya-Michel and Castellanos-Villegas 2011; Celaya-Michel et al. 2015), soil carbon accumulation (Castellanos et al. 2010; Morales-Romero et al. 2015), and soil moisture distribution, recharge, and availability in the soil profile (Castellanos et al. 2016). Water availability after prolonged rainfall periods increases in the soil profile under buffelgrass canopies, because of their limited rooting depth, and can be used by the remaining deep-rooted dominant tree and shrub species. Increasing the storage and availability of water in the deeper soil profile of the savanna (Fig. 23.2) decouple rainfall season and the time of water use by the remaining species and extend the amount of time during the year in which the species remain productive (Hinojo-Hinojo et al. submitted). It is noteworthy that changes in land cover and disturbance will reduce shallow water consumption and increase infiltration and volumetric soil moisture deeper in the soil profile. Increase in deeper soil moisture in subtropical drylands decouple plant activity from rainfall periods and extend the period of photosynthetic carbon gain and ecosystem productivity of deep-rooted perennial shrubs and trees (Scott et al. 2006, 2014), when other environmental factors like below zero temperatures or cloudiness are not limiting. Some species of dominant tree species in the drylands of Mexico are known to help redistribute water from deep to shallow roots and facilitate the growth and activity of annual and herbaceous perennial plants (Hultine et al. 2003, 2004).

23.4 Ecophysiological Tolerance of Ferns in the Cloud Forest

23.4.1 *The Cloud Forest*

Low and often-twisted deciduous and evergreen trees and high abundance and biomass of epiphytes characterize the cloud forest (Hietz and Hietz-Seifert 1995; Crausbay and Martin 2016). Cloud forest is distributed in fragmented form

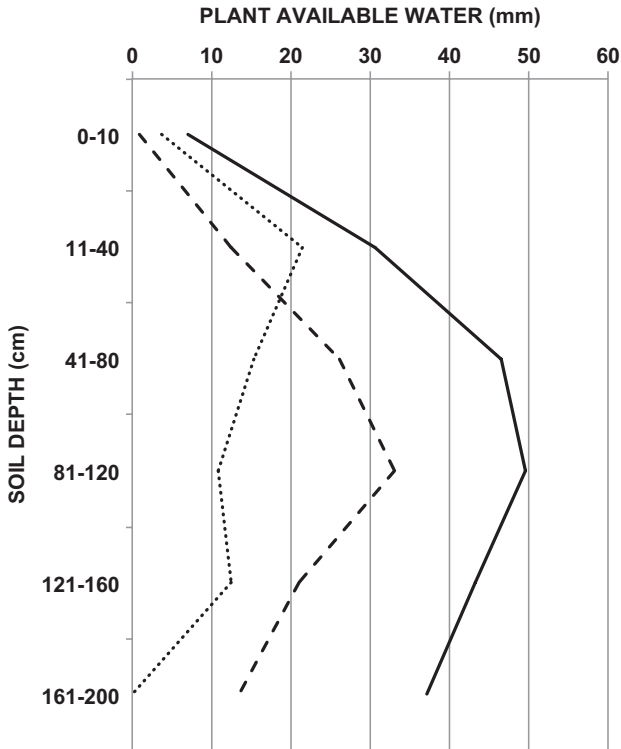


Fig. 23.2 Plant available water (mm) in the soil profile under the canopy of *Olneya tesota* (ironwood) in native (dashed) and disturbed (pointed) sites and *Cenchrus ciliaris* (buffelgrass, solid line) after the rainfall season (2012). Values result from the integration of 10 cm depth intervals

between 1000 and 3500 m of altitude, in rainy and cold mountains with high frequency of clouds and mist that limit the incidence of sunlight inside the forest (Lüttge 2008). Cloud forest collects large amounts of rain; however, there are periods without rain that can last several weeks and cause seedling mortality (Engelbrecht et al. 2005).

Climate changes and human disturbances have affected the distribution and decreased the extension of cloud forest (Foster 2001; Crausbay and Martin 2016). It has been predicted that the cloud forest will change to new climatic zones, but it will not move as a unit because it is composed of many species and possibly each one will respond in a particular way to the human-induced global change. However, the data commonly used to model the potential distribution of the species is made with average values of the climate, without taking into account the physiological tolerance of the plants to the physical conditions of the microhabitat, which can differ substantially from the regional climate (Foster 2001; Zotz and Bader 2009). Therefore, an important task is to know the physiological responses of plants to the environmental conditions of the ecosystems where they live.

23.4.2 *Ecological Groups of the Ferns in the Cloud Forest*

Light intensity is one of the most important environmental factors that influence the abundance, growth, and survival of plants in Tropical Mountain Forests (Poorter and Arets 2003; Lüttge 2008). Different light environments caused by the fall of trees and edges of the forest favors the coexistence of species with different light requirements (Chazdon et al. 1996). Shade-tolerant plants have low phenotypic plasticity in response to changes in the light environment, compared to sun-tolerant plants. Shade-tolerant plants show low photosynthetic and respiration rates and are slow growing, while light-demanding plants show higher photosynthetic and respiration rates and are fast growing (Chazdon and Smith 1996; Poorter and Arets 2003). In addition, the species are able to acclimatize physiologically to the seasonal climatic changes of the Tropical Mountain Forests (Chazdon et al. 1996). In ferns, interspecific differentiation in the response of the spore to the physical environment and tolerance to desiccation in the gametophyte has been associated with the preference of the habitat of the sporophyte (Pérez-García et al. 1982; Watkins et al. 2007; Testo and Watkins 2013; Riaño et al. 2015). Similarly, differences in distribution and physiological response between sporophytes of fern species that inhabit the same community support the hypothesis that the differentiation of niches promotes the coexistence of species (Hietz and Briones 1998; Arens and Sánchez-Baracaldo 1998; Durand and Goldstein 2001; Saldaña et al. 2010; Volkova et al. 2009, 2010; Bystrakova et al. 2011; Riaño and Briones 2013, 2015).

Several authors have made contributions to recognize functional groups in ferns. In the middle of the last century, the ferns of Singapore and Malaysia were divided according to the habitat where they grow in terrestrial sun, terrestrial shadows, rocks, banks of gullies, aquatic, and mountain species (Holtum 1954). The physiological behavior of terrestrial cloud forest ferns characterizes them as shade plants because they tend to show low photosynthetic and respiration rates and are slow growing (Chazdon and Smith 1996; Poorter and Arets 2003). It has been hypothesized that the tolerance of ferns to low light environments is due to the action of phytochrome PHY3 and neochrome, because both photoreceptors are sensitive to blue and red light (Kawai et al. 2003; Li et al. 2014). However, there are important differences between species of tropical terrestrial ferns in the distribution and degree of shade tolerance (Durand and Goldstein 2001; Jones et al. 2007; Bystrakova et al. 2011; Riaño and Briones 2013, but see Volkova et al. 2010). In a cloud forest where several species of ferns coexist, the arborescent fern *Alsophila firma* was abundant in gullies and humid sites, the arborescent *Cyathea divergens* and the herbaceous *Blechnum schiedeanum* occupied moderately open sites, while the arborescent *Lophosoria quadripinnata* and the herbaceous *B. appendiculatum* preferred more open sites (Riaño and Briones 2013; López-Romero et al. 2016).

With respect to humidity, epiphytic species have been grouped into poikilohydric and homohydric hygrophytes, mesophytic, and xerophytic that tolerate drought or evade it (Benzing 1990). In relation to light, the epiphytes have been categorized as exposed with total or almost total exposure to the sun, sun with growth in half shadow

and shade-tolerant to deep shadow (Pittendrigh 1948; Benzing 1990). The epiphytic species in the cloud forest prefer different zones in the sporophyte. These zones are distinguished by their height, thickness, and inclination of the branches and composition of the substrate accumulated in the branches (Johansson 1974; Kelly 1985; Ter Steege and Cornelissen 1989; Hietz and Hietz-Seifert 1995; Hietz and Briones 1998; Rudolph et al. 1998). The distribution of the biomass of the epiphytic fern species in a cloud forest was unequal in the sporophyte and allowed to classify them based on their apparent luminance requirement (Hietz and Briones 1998). The deep shade-tolerant type composed of *Trichomanes bucinatum* and *Asplenium cuspidatum* showed 85–100% of the biomass confined to the base and bark of the trunks. The sun type or tolerant to medium shade formed by *Elaphoglossum glaucum*, *E. petiolatum*, *Phlebodium areolatum*, and *Polypodium puberulum* distributed 80–100% of its biomass in the upper trunk and branches thick >20 cm and medium thick >5 cm diameter. The exposure type was composed of *Pleopeltis mexicana* and *Polypodium plebeium* with 70–95% of its biomass on relatively thick branches of 5–20 cm and thin <5 cm in diameter (Hietz and Briones 1998).

23.4.3 Ecophysiological Tolerance of Ferns of the Cloud Forest

The spore, gametophyte, and sporophyte are the most important phases of the life cycle of the ferns (Sharpe and Mehltreter 2010). The spore is a haploid cell dispersed by the wind, but due to its small size (25–50 μm), it can remain in the pores of the soil and keep dormant forming a bank of spores (Pérez-García et al. 1982; Sharpe and Mehltreter 2010). The gametophyte is a laminar and tiny plant with rootlets, without vascular tissue or stomata, has little capacity to store water, and can be poikilohydric but requires water for fertilization, while the sporophyte is a conspicuous perennial plant, with vascular tissue, rhizome, roots, and leaves with stomata and sori (Farrar et al. 2008; Watkins et al. 2010). Due to these differences, the sporophyte and gametophyte can have independent environmental tolerances and optimally succeed in different habitats (Warne and Lloyd 1980). The physiological limitations of the ferns determine that many species grow under the shade of the canopy or in humid places of the cloud forest (Hietz and Briones 1998; Riaño and Briones 2013; López-Romero et al. 2016). However, ferns are physiologically competitive and have a large number of adaptive characters resistant to abiotic stress, so that they can colonize shady sites, as well as open areas and can survive in flooded and degraded lands (Hietz and Briones 2004; Hietz 2010; Mehltreter et al. 2010; Watkins et al. 2010).

23.4.3.1 Ecophysiological Tolerance of the Spore Germination

Light and water are the resources that mostly limit the germination of the fern spores, and their success in germinating has an important influence on the distribution of the species. The spores of species whose sporophytes grow in shade environments germinate better in conditions similar to the interior of the forest, such as lower

temperature, low light, and high availability of water, while those that are distributed in open or exposed environments germinate in higher values of temperature, light, and water availability (Warne and Lloyd 1980; Pérez-García and Riba 1982; Riaño et al. 2015; López-Romero et al. 2016). The light promotes the germination of the spores of the ferns through a system of phytochromes. Phytochrome-dependent germination can be photoreversible with a far-red irradiation and can be photoreversible by brief irradiation with blue or UV light (Raghavan 1989). With the phytochrome system, the spore detects light in the gaps forest and the proximity to the soil surface, which allows the spores to germinate under favorable conditions for the growth of the gametophyte and sporophyte (Pérez-García et al. 2007). No spores germinated under far-red light or darkness; but germination was high under white light in four species of tropical ferns (Pérez-García et al. 2007). The temperature for the germination of fern spores ranges between 15 and 30 °C, and the optimum germination temperature of five arborescent species was 25 °C (Pérez-García and Riba 1982). *Lophosoria quadripinnata* and *Trichipteris bicrenata* had the highest tolerance to extreme temperatures in a thermal gradient of 11–35 °C, while *Trichipteris scabriuscula* had the lowest tolerance; *Nephelea mexicana* and *Cyathea fulva* had an intermediate tolerance (Pérez-García and Riba 1982). The spores of *Alsophila firma*, *Lophosoria quadripinnata*, and *Cyathea divergens* seeded at 13 °C, 21 °C, and 25 °C increased germination with the increase in temperature, but *L. quadripinnata* had higher thermal tolerance compared to *A. firma* and *C. divergens* (Salvador 2014). In six ornamental fern species, it was found that the best substrate for germination was the mixture of peat pH 6 and perlite, reaching 100% germination of *Cyathea cooperi*, *Pteris cretica*, and *P. incompleta*, but with mixture of peat pH 4 and perlite germination decreased significantly in *Cyathea cooperi*, *C. contaminans*, and *C. tsangii*, and the lowest germination percentages of all species, including *Asplenium nidus*, were obtained in sand substrate (Barros et al. 2008). In *Dryopteris munchii*, twice as many gametophytes were obtained in spores germinated in soils derived from volcanic toba, in comparison with those obtained in chromic luvisol soil (Jaramillo and Mendoza 2004).

The differences observed in the frequency of individuals in the understory and the correspondence of the spore's physiological behavior with respect to water availability support the hypothesis that the coexistence of five sympatric species in a cloud forest occurs by differentiation in the ecological niche from early stages of the individual's development (Riaño et al. 2015; López-Romero et al. 2016). The germination of the spore of the herbaceous species *Blechnum appendiculatum* and *B. schiedeanum* and the arborescent tree ferns *Alsophila firma*, *Lophosoria quadripinnata*, and *Cyathea divergens* was controlled by exposure to light and water availability. The spores of all the species did not germinate under darkness, and the germination was smaller with far-red light, compared with white light. All species germinated at very low photon flux density ($0.04 \mu\text{mol m}^{-2} \text{s}^{-1}$) and increased germination with the amount of light received, but the saturation of germination was different between species. The decrease in available water from 0 to -0.7 MPa reduced germination in all species, and the water requirements for germination were associated with the habitat preference where sporophytes grow. The increase in canopy opening from 0.6% to 19.1% decreased the germination capacity of the three species of tree ferns, but *L. quadripinnata* was the least affected (Riaño et al. 2015).

23.4.3.2 Ecophysiological Tolerance of the Gametophyte

The gametophyte of a fern may have a broader environmental tolerance than its sporophyte and is physiologically similar to the gametophyte of a bryophyte (Ong et al. 1998; Farrar et al. 2008). The distribution of fern gametophytes depends on multiple environmental conditions and resources, and disturbance is also important (Farrar et al. 2008). In sites with low light and no disturbance in a humid forest, no gametophytes were established, while in high light sites, the density of gametophytes was increased by the removal of the litter and when the topsoil layer was removed and exposed (Watkins et al. 2007). The gametophytes of the arborescent ferns *Alsophila firma*, *Cyathea divergens*, and *Lophosoria quadripinnata* when they grew with 42% and 85% solar radiation in shade houses and with 7% and 23% of solar radiation in the understory of a cloud forest decreased the quantum yield (proportion of the light used in photosynthesis) and increased the electron transport rate of photosynthesis in treatments with higher solar radiation; however, solar radiation decreased the survival of the three species, and *L. quadripinnata* had higher survival in comparison with *A. firma* and *C. divergens* in the shade house with higher solar radiation (Salvador 2014). Gametophytes of the same three species subjected to >96% RH did not reduce the quantum yield, but it decreased strongly to 69% and 35% of relative humidity and gametophytes tolerated direct solar radiation up to 30 min (Riaño and Briones 2015). The high dependence of gametophytes from tree ferns to humid environments could explain why these species, and possibly other species with similar life histories, are restricted to humid forests (Bystriakova et al. 2011; Ramírez-Barahona et al. 2011; Riaño and Briones 2015).

In comparison with the sporophyte, there have been very few studies on the photochemistry and carbon metabolism in the gametophyte. The CO₂ assimilation rate of the gametophytes of four fern species (of the genera *Cibotium*, *Todea*, *Pyrrosia*, and *Thelypteris*) ranged between 0.03 and 0.18 μmol CO₂ g⁻¹ s⁻¹ (Farrar et al. 2008). Photosynthetic rate of the gametophyte could be compared with that of a young sporophyte in an epiphytic fern, obtaining values of 0.18 and 0.14 μmol CO₂ g⁻¹ s⁻¹, respectively (Sakamaki and Ino 1999). The gametophyte of 15 fern species recovered their physiological functioning after dehydration, and the capacity for recovery was variable among the species (Farrar et al. 2008). The quantum yield of the gametophyte of an epiphytic fern species that grew in exposed environments recovered almost completely after 24 h of desiccation, while it decreased strongly in the same period of desiccation in another species of terrestrial fern that inhabited shaded sites (Farrar et al. 2008). The gametophytes of the tropical epiphytic ferns *Phlebodium pseudoaurum* and *Microgramma reptans* recovered the initial values of quantum yield after exposure to treatments of low relative humidity; however, the gametophytes of *Diplazium striatastrum*, a terrestrial species that grows in humid environments within the forest, were unable to recover their quantum yield values (Watkins et al. 2007). The gametophyte of *Asplenium scolopendrium* var. *americanum*, a rare species with low abundance in a Temperate Forest, could not tolerate a relative humidity <90%, in comparison with other species of the same genus and common in the same forest that presented physiological tolerance to desiccation (Testo and Watkins 2013).

These authors attributed interspecific differences in relative humidity tolerance to habitat preference among species. The gametophytes of *Asplenium trichomanes*, *A. scolopendrium*, and *Ceterach officinarum* showed similar capacity to acclimate their photosynthetic apparatus to the increase of the quantity of light modifying the content of photoprotective pigments (Fernández-Marín et al. 2012). The pigments of the gametophytes of these three species were not qualitatively different from those of the sporophytes of seven species of epiphytic ferns (Tausz et al. 2001).

23.4.3.3 Ecophysiological Tolerance of the Sporophyte

The sporophyte leaf of ferns behaves like the leaf of other vascular plants (Hietz and Briones 1998; Watkins et al. 2010). The cuticle and stomata of the leaves of the sporophytes help them to avoid the loss of water, but the low capacity to drive and store water causes restrictions to the transpiration and carbon gain, in comparison with the angiosperms (Woodhouse and Nobel 1982; Watkins et al. 2010).

Chlorophyll fluorescence data show that the sporophyte leaf possesses quantum yield values and electron transport rates similar to the other vascular plants (Maxwell and Johnson 2000). The maximum quantum yield or predawn yield of the arborescent cloud forest ferns is at the optimum value of most non-stressed plants and is similar to the arborescent ferns of humid forests, non-arborescent terrestrial ferns of tropical and humid forests, and epiphytic ferns of tropical forests (Durand and Goldstein 2001; Zhang et al. 2009; Huang et al. 2011), but it is slightly larger than that of arborescent ferns of sclerophyllous moist forests (Volkova et al. 2010). On the other hand, the maximum quantum yield of the unstressed fronds of the epiphytic ferns of a cloud forest was scarcely less than that of tree ferns coexisting in the same forest and of epiphytic ferns in a tropical rainforest (Zhang et al. 2009). The apparent maximum rate of electron transport (ETR_{max}) of the tree ferns *Alsophila firma*, *Cyathea divergens*, and *Lophosoria quadripinnata* of a cloud forest was low compared to species of environments with high light availability, such as semi-deciduous rainforests and sandy coasts (Geßer et al. 2005, 2008; Riaño and Briones 2013) and sun ferns (Wong et al. 2012); however, they showed similar values to the highest values of ETR or ETR_{max} of arborescent and herbaceous ferns of the temperate rainforest and temperate evergreen forest (Bystriskova et al. 2011; Saldaña et al. 2010; Wong et al. 2012). The ETR light saturation values of the tree ferns *Alsophila firma*, *Cyathea divergens*, and *Lophosoria quadripinnata* of a cloud forest were lower than those of sunny environments (Geßer et al. 2005, 2008; Riaño y Briones 2013) but similar to those of three species of the genus *Blechnum* growing in an open canopy in a temperate evergreen forest (Saldaña et al. 2010).

The CO₂ assimilation rate of sporophytes ranges between 0.6 and 15 μmol m⁻² s⁻¹, which is similar to that of vascular shade plants (Hietz and Briones 2004; Hietz 2010; Mehltreter et al. 2010). The maximum photosynthesis (A_{max}) of three tree fern species of a cloud forest was higher than A_{max} of the moss, similar to that of other terrestrial fern species occupying closed sites and shaded leaves of deciduous trees, and less than that of tree ferns of the humid forest, epiphytes of exposed sites, and

tropical and herbaceous trees C_3 and C_4 (Durand and Goldstein 2001; Larcher 2003; Hietz and Briones 2004; Lüttge 2008; Volkova et al. 2010; Riaño and Briones 2013). The Amax of the epiphytic ferns of the deep shadow group of a cloud forest was similar to that of mosses, shadow epiphytes, and terrestrial ferns of closed sites, while the Amax of the epiphytic ferns of the exposure group was similar to other epiphytes of the same group and the Amax of the epiphytic ferns of the exposure and tolerant groups was similar to the Amax of terrestrial ferns of closed sites and shade leaves of deciduous and tropical trees (Hietz and Briones 2001). Zhang et al. (2009) also found no differences in Amax between two species of epiphytic ferns and two species of terrestrial ferns in a tropical rainforest. Riaño and Briones (2013) showed that the density of photosynthetic flux to saturation of photosynthesis (PPFDsatA) of tree ferns *Alsophila firma*, *Cyathea divergens*, and *Lophosoria quadripinnata* of a cloud forest growing in a closed site was similar to that of shade plants, other terrestrial and arborescent ferns of closed sites, and shadow epiphytes, indicating the efficiency of tree ferns to absorb the scarce available light and assimilate CO_2 in shaded habitats by the canopy (Durand and Goldstein 2001). The PPFDsatA of the epiphytic ferns of a cloud forest was higher than that of shade plants and terrestrial ferns of closed sites, but the light compensation point (LCP) of the epiphytic ferns was similar to that of both groups (Hietz and Briones 2001). Despite their low photosynthetic rate, possibly the result of a deficiency of nutrients, the high PPFDsatA values of the epiphytic ferns of the cloud forest allow them to take advantage of high amounts of light in the hours or areas with high light in the canopy. On the other hand, the low LCP values of the epiphytic ferns make it easier for them to assimilate carbon during the frequent cloudy days or when they grow in shaded places in the canopy forest (Briones and Hietz 2001). Three herbaceous ferns of the genus *Blechnum* of a temperate forest that differ in the range of the light environment that they occupy in the undergrowth adjusted the leaf area in correspondence with the habitat that they occupied, being more plastic the species with greater ecological amplitude, but they did not show differences in the rates of CO_2 assimilation and respiration in the dark (Saldaña et al. 2010). In a New Zealand tropical forest, two tree ferns with a fast height growth rate of the genus *Cyathea* had high electron transport rates, in comparison with two species of the same genus and *Dicksonia squarrosa* (Bystriakova et al. 2011).

Like other plant species, the arborescent ferns of the cloud forest respond to the decrease in water availability by decreasing their water potential, possibly due to the increase in transpiration and/or decrease in water conduction by the stems, and their leaves thickening in the dry season (Riaño and Briones 2013). The decrease of the hydric state of the arborescent ferns of the cloud forest can be caused by the relatively high temperature and evaporative demand of the air during the dry season, in addition to the decrease of the hydric potential of the soil. However, even in the dry season, the soil water potential of a cloud forest can remain high, between -0.01 and -0.26 MPa. The decrease in water potential of the arborescent ferns *Dicksonia antarctica* and *Cyathea australis* of a sclerophyllous wet forest in response to the sudden exposure of high levels of light was not associated with changes in water availability, but probably with an increase in transpiration due to the increase in leaf

temperature and possible decrease in water conduction (Volkova et al. 2009). The epiphytic ferns of a cloud forest that tolerate deep shade and grow at the base of the trunks showed no obvious adaptations to cope with drought (Hietz and Briones 1998). The leaves of *Trichomanes bucinatum* were completely dried after a few hours in moderately dry air, and the low ability to contain water caused the quantum yield to decrease faster compared to the epiphytes that grow in more exposed sites (Hietz and Briones 2001). Despite losing more than 90% of the relative water content, the quantum yield of *T. buccinatum* was able to return to half its capacity in less than 5 min and up to 90% after 1 h. Most of the plants that inhabit the canopy show adaptations to the xeric environment (Benzing 1990). The shade-tolerant and exposure-tolerant epiphytic ferns of a cloud forest showed leathery leaves, succulent rhizomes, low rates of uncontrolled water loss, leaf scales, and high cellular elasticity (Hietz and Briones 1998). The flow of water from the atmosphere to the leaves could be an important source of water for cloud forest ferns, but the cuticle of the leaves being very efficient for the control of water loss could be limiting for the absorption of liquid water or water vapor. Both the epiphytic ferns of the tolerant type and the exposure type of the cloud forest showed values of total water potential similar to those of the epiphytic bromeliads (Hietz and Briones 1998). The epiphytic ferns of the exposure type of a cloud forest diminished their values of total water potential in response to the drought, in comparison with the ferns of the tolerant shade type (Hietz and Briones 1998). Most vascular plants close their stomata before loss of cell turgor with increasing drought; however, the epiphytic ferns of the exposure group of a cloud forest had the capacity to tolerate the loss of water beyond the point of turgor loss before the stomatal closure (Hietz and Briones 1998).

In conclusion, the spores of the ferns have mechanisms to detect the environment and initiate germination when conditions are favorable in the cloud forest. The specialization to humid habitats of the gametophyte of tree ferns possibly restricts the distribution of that group to humid places. The physiological tolerance of the gametophytes of the epiphytic ferns of the cloud forest is practically unknown. The differences in the plasticity and relatively high physiological tolerance of the sporophyte facilitate the coexistence of the fern species in the cloud forest. The physiological performance as shade plants of terrestrial and epiphytes ferns makes them vulnerable to fragmentation and changes in the use of the land in the cloud forest.

23.5 Functional Diversity in the Tropical Rainforest: *Piper*, a Case Study

The tropical rainforest (TRF) is one of the most complex ecosystems and supports the highest biodiversity and productivity on earth. This forest is found along the equatorial region, where climate is more stable, hot, and wet. In Mexico, TRF has an extension of 91, 566 km² (4.7%), representing 45% of its original surface. Since 1960 its importance as a natural resource and the high rate of fragmentation and decrease of its original surface raised the necessity to study the biodiversity and the

dynamics of change and regeneration of the TRF as the basis for restoration and conservation alternatives.

Natural disturbance, produced by gaps formation, and succession of TRF are dynamic processes in which spatial and temporal variability of the light environment plays a fundamental role, becoming a selective factor for plant attributes of these communities. To understand these processes, in 1970, Gómez-Pompa et al. initiated a series of ecological and ecophysiological pioneer studies of TRF plants at “Los Tuxtlas,” a biological reserve in Veracruz, Mexico, and proposed a model to study its dynamics and to establish the scientific basis for future conservation (Gomez-Pompa et al. 1972). The theoretical framework of the research was published in the paper “The tropical rainforest: a non-renewable resource” published in 1972. The approach to fulfill their goal included ecological and physiological studies of species with differential distribution in diverse successional stages. Considering the high biodiversity of the TRF, they selected a group of species of the genus *Piper* as a model system to understand functional diversity and its ecological importance (Gómez-Pompa et al. 1976; Gómez Pompa and del Amo 1985; Field and Vázquez-Yanes 1993).

Piper species have a worldwide distribution, containing a high number of species. At “Los Tuxtlas” reserve, *Piper* has 12 species differentially distributed in habitats with variable light availability and successional stages (Gómez-Pompa 1971; Fig. 23.3), becoming a good system to study the mechanisms underlying the distribution of TRF species, as well as the ecological and evolutionary meaning of

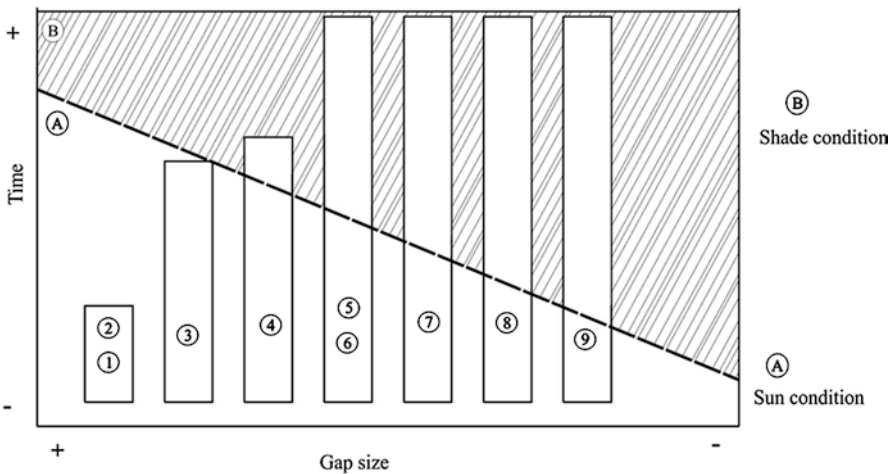


Fig. 23.3 Temporal and spatial distribution of nine *Piper* species of the tropical rainforest at Los Tuxtlas, Veracruz, Mexico. The bar indicates the amplitude of distribution of the species under different light environments along time and gap size axis. Species are indicated by numbers: (1) and (2) *Piper umbellatum* and *P. peltata*, (3) *P. auritum*, (4) *P. aduncum*, (5) and (6) *P. hispidum* and related forms of the species, (7) *P. amalago*, (8) *P. lapathifolium*, and (9) *P. aequale*. (Figure modified from Gómez-Pompa and Vázquez-Yanes 1985)

physiological and morphological responses of plants to light (Gómez-Pompa et al. 1971; Field and Vázquez-Yanes 1993). The studies initiated addressing the ecophysiology of germination and further were diversified to several topics including seedlings survival, establishment, photosynthesis, mineral nutrition, and growth (Vázquez-Yanes 1976, 1985; Field and Vázquez-Yanes 1993). These studies generated a great interest for ecophysiological studies of the TRF plants in Mexico and other countries (Denslow et al. 1990; Field and Vázquez-Yanes 1993; Nicotra et al. 1997). Furthermore the studies provide the basis for understanding the mechanisms of TRF species for adaptation to different rainforest habitats and their relation with the species distribution and role in ecological succession.

23.5.1 *Physiology of Germination*

Tropical rainforest pioneer species produce small seeds that may persist in the rainforest floor, until a canopy disturbance originates a gap and favorable conditions for their germination and establishment. The studies of germination of *Piper*, and other pioneer species from Los Tuxtlas Veracruz, in response to light and temperature clearly establish the role of light quality and temperature on the control of germination of photoblastic species (Vázquez-Yanes and Smith 1982). The studies have also provided a better understanding of the mechanisms of light use and acclimation in TRF plants, as well as its importance for species distribution in different successional stages (Vázquez-Yanes and Orozco-Segovia 1987, 1990).

Piper species produce a large number of small seeds with specific light requirements for germination. The seeds are nondormant after dispersal, and under appropriate light, temperature and humidity conditions may germinate immediately. However, if seeds are dispersed in the rainforest floor or buried in the soil, germination is inhibited by enforced dormancy and remains viable for more than 1 year, until light and/or temperature conditions trigger germination (Orozco-Segovia and Vázquez-Yanes 1990; for a review see Vázquez-Yanes and Orozco-Segovia 1993). Photoblastic seeds sense the light environment through phytochrome pigments, which function as a signal-transducing photoreceptor of light quality. Phytochrome has two forms: an active form (Pfr) and one inactive (Pr) which are interconverted by the amount of red and far-red light in the environment (R/FR ratio); this ratio increase when canopy opens, triggering seed germination, and modulating development and growth of plants (Vázquez-Yanes and Smith 1982; Orozco-Segovia and Vázquez-Yanes 1989).

In mature forest, when the canopy opens by natural or anthropogenic disturbance, changes in the daily temperature alternation in the soil and changes in the amount and quality of the light reaching the ground are detected by seeds. The fine perception sensing these changes in their surroundings allows the seeds to recognize the arrival of specific favorable conditions for germination and establishment (Vázquez-Yanes 1976; Vázquez-Yanes and Orozco-Segovia 1993).

Although for germination and establishment all *Piper* species are triggered by light, seeds of pioneer trees common in secondary forest such as *Piper auritum*, *P. sanctum*, *P. aduncum*, *P. marginatum*, *P. umbellatum*, and *P. aff. yzabalanum* require large gaps for dormancy break and germination. On the other hand, *P. lapathifolium*, *P. nitidum*, and *P. amalago*, species common in mature forest, have partial photoblastism, larger seeds, and short viability. *Piper hispidum* is the more plastic species; its seeds germinate in a wide range of light conditions, from shade of the understory to secondary forest, and it can be found in all these successional stages (Vázquez-Yanes and Orozco-Segovia 1982; Orozco-Segovia and Vázquez-Yanes 1989).

Piper seedlings growth rates also reflect their differential ability to develop under contrasting light conditions. A study on growth responses of *P. aequale*, *P. auritum*, and *P. hispidum* seedlings to contrasting natural and experimental light environments reveals that *P. auritum* had the best growth response under high light; *P. aequale* grew better at intermediate light levels, whereas *P. hispidum* showed more plasticity and grew well along the whole range of light conditions (Sanchez-Coronado et al. 1990). This study reveals how the species have a different degree of adaptation in physiological traits to germinate and grow in gaps of different size.

23.5.2 *Photosynthesis and Light Environment*

The light environment of the TRF is characterized by high spatial and temporal variability. The light varies from full sun in large gaps, open areas, and top of the canopy to less than 5% of full sun in the understory; spatially, light levels also varied according to gaps size. Although understory is characterized by low light conditions, short periods of direct light (sunflecks) that pass through the canopy openings reach the plants, making their light environment highly dynamic with a widely temporal variation, from few seconds to minutes; sunflecks also present a high variation in peak photon flux density (Chazdon 1988).

Photosynthetic capacity among *Piper* species varied according to their ability to grow under different light conditions (Walters and Field 1987; Chazdon et al. 1989). Large gap species show leaves with the highest photosynthetic capacity, taking advantage of the high light found in these environments; this capacity is combined with high leaf area, high nitrogen content, and short leaf life span (<1 year). On the other hand, understory species have leaves with the lowest photosynthetic capacity, small area, lower nitrogen content, and longevity of 3–5 years (Chazdon et al. 1989, Table 23.3). Differences among species in the way they gain and invest their resources allow *Piper* species to fall in a continuum between photosynthetic maximization on one side and cost maximization on the other (Field and Vázquez-Yanes 1993). *P. hispidum*, one of the species with wider distribution in different light conditions, produced leaves with photosynthetic and cost features nearly along the entire range; leaf longevity also showed plasticity lasting from 6 months to 2 years (Field and Vázquez-Yanes 1993).

Table 23.3 Photosynthetic, structural, and environmental characteristics of leaves of six *Piper* species

Characteristic	Species					
	<i>P. aequale</i>	<i>P. amalago</i>	<i>P. lapathifolium</i>	<i>P. auritum</i>	<i>P. hispidum</i> Clearing	<i>P. umbellatum</i>
Amax/area ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)	2.61 ± 0.08	2.65 ± 0.16	3.04 ± 0.13	9.53 ± 0.50	9.61 ± 1.29	6.14 ± 1.16
Amax/mass ($\text{nmol CO}_2 \text{ g}^{-2}\text{s}^{-1}$)	71.80 ± 1.93	73.95 ± 5.08	97.05 ± 3.17	344.75 ± 21.82	192.61 ± 26.63	87.86 ± 37.66
PPNUE ($\text{mol CO}_2 \text{ N}^{-2}\text{s}^{-1}$)	36.16 ± 1.24	43.09 ± 2.47	49.61 ± 1.51	126.65 ± 5.75	90.07 ± 9.70	92.16 ± 11.44
N/area (mmol N m^{-2})	72.45 ± 1.15	61.60 ± 1.12	61.13 ± 1.43	74.84 ± 1.76	102.41 ± 4.31	64.95 ± 6.02
N/mass (mmol N g^{-2})	1.99 ± 0.05	1.70 ± 0.04	1.95 ± 0.02	2.68 ± 0.07	2.02 ± 0.09	1.97 ± 0.21
LSM (g m^{-2})	36.46 ± 0.89	36.26 ± 0.71	31.29 ± 0.78	28.06 ± 0.68	51.52 ± 2.09	33.21 ± 90.93
Canopy openness for leaf (%)	6.58 ± 0.61	4.53 ± 0.28	5.14 ± 0.34	35.20 ± 1.71	23.74 ± 2.96	20.77 ± 3.26
Measured daily PFD ($\text{mol m}^{-2} \text{ d}^{-1}$)	0.36 ± 0.09	0.70 ± 0.16	0.41 ± 0.04	13.54 ± 1.39	9.44 ± 1.86	15.28 ± 2.72

Table modified from Chazdon and Field (1987)

Values are means ± s.e

Amax: maximum assimilation rate, PPNUE: photosynthetic nitrogen use efficiency, LSM: leaf-specific mass, N: nitrogen content, PFD: photon flux density

Sunflecks represent an important resource for understory plants, as they provide 10–80% of the total photon flux density available for photosynthesis (Chazdon 1988). For *Adenocaulon bicolor*, an understory herb, 30–70% of the total daily carbon gain occurs during sunflecks (Pfitsch and Pearcy 1989). Therefore the capacity of understory plants to utilize this resource may have a strong influence on their growth and reproduction (Pfitsch and Pearcy 1989).

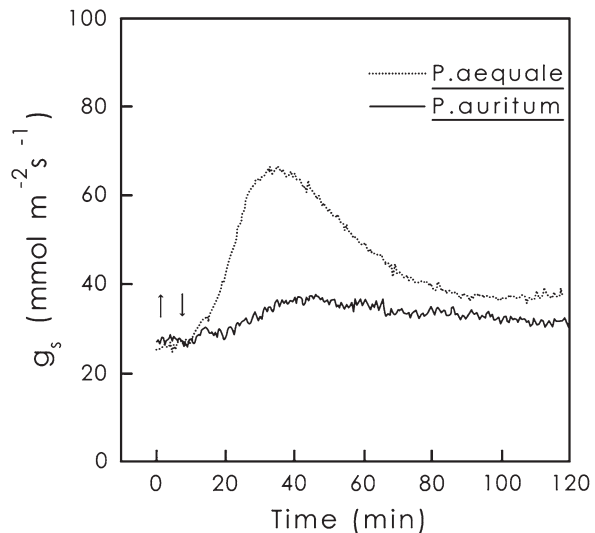
The ability of plants to utilize sunflecks depends, at a physiological time scale, on the photosynthetic induction state, a process determined by the response dynamics of photosynthetic enzymes and stomatal opening. The completion of the induction process may last 20 min under continuous high light, but it may be able to be attained under dynamic light conditions (Pearcy 1990). When a sunfleck arrives at the leaf surface of an understory plant, an increase in CO₂ assimilation occurs, and it continues for at least 1 min after the sunfleck has passed as post illumination CO₂ fixation; the state of induction before the sunfleck determines the maximum assimilation rate during the sunfleck (Pearcy 1990).

The role of dynamic stomatal and biochemical responses to variable light on carbon gain was studied in two *Piper* species with contrasting distribution: the pioneer tree, *P. auritum*, and a shade-tolerant shrub, *P. aequale*. The species were acclimated to high and low light to determine the influence of photosynthetic acclimation on dynamic photosynthetic responses.

Results showed that acclimation to contrasting light environments had a significant effect on stomatal response dynamics; for both species, the integrated stomatal conductance (g_s) response to lightflecks was smaller when plants were acclimated to a light regime different to its natural environments (Tinoco-Ojanguren and Pearcy 1992, Fig. 23.4).

The steady-state and the dynamic responses of CO₂ assimilation (A) and g_s to light (light curves and lightflecks, respectively) showed contrasting results; for

Fig. 23.4 Representative time course of the stomatal responses, of shade-acclimated plants, to a lightfleck of 4 min duration. Arrows indicate the time when PPFD was increased and decreased



shade-acclimated plants, the steady-state responses were identical; in contrast, the response to lightflecks was significantly different (Tinoco-Ojanguren and Pearcy 1992). The shade-tolerant species *P. aequale* showed larger and faster g_s response than the gap species *P. auritum*. The response of *P. aequale* allowed this species to keep higher g_s and intercellular CO_2 concentration during a series of consecutive lightflecks and therefore improves assimilation by 30–200%, depending on the sunfleck duration. In comparison, the gap species presented a small stomatal response to lightflecks and no improvement in C gain. In contrast for high light-acclimated plants, g_s response to lightflecks was greater in *P. auritum* than *P. aequale*.

Vapor pressure deficit (VPD) had a significant effect on the stomatal response to lightflecks. Increases in VPD had decreased the magnitude and dynamics of the response, exhibiting a more conservative behavior in terms of water loss, at the expenses of carbon gain. The effect was different among species and between sun- and shade-acclimated plants. Sun plants of *P. auritum* were more sensitive to VPD (Tinoco-Ojanguren and Pearcy 1993). These results suggest a possible adaptive significance of the stomatal response for the species studied. Shade-acclimated plants of *P. aequale* showed a stomatal response that would be expected for a species that maximize C gain in an environment where light is the main limiting factor. Sun acclimated plants of *P. auritum* had a stomatal behavior that would be expected for a species that maximizes C gain and water loss in an environment where light is not limiting but water stress may be an important limitation.

23.6 Implications of Functional Diversity in Conservation

The case studies presented in this chapter are just an example of plant functional diversity found at different phases of their life cycle and at different complexity levels. There is still the necessity for increasing our knowledge to predict how climatic change, fragmentation, land use change, introduction of exotic plants, and other anthropogenic disturbances are affecting most species directly or indirectly, as many biotic interactions are affected by these disturbances. The importance of knowledge on functional traits for conservation issues has led to propose a research discipline: conservation physiology, which has been defined in a broad sense as a scientific discipline that encompasses functions and mechanisms at all scales (from molecules to biosphere) and their responses to environmental changes; it also includes the development of strategies to understand, manage, and restore populations and ecosystems (Cooke et al. 2013). This definition assumes that for real advancements in conservation and resources management, this discipline must also be integrative with other disciplines. In a rapidly changing world, efforts should be focused to the responses of plant species (including invasive species) to environmental changes to develop models for well-characterized functional diversity for management and restoration proposals, especially for keystone species, vulnerable species such as epiphytes, rare and endemic species, and some seedlings that require host trees and nurses.

Mexico has provided to the world several globally important cultivated plants such as maize, beans, cacao, prickly cactus, and tomato, which are the result of selection from its high plant diversity, together with the empirical botanical knowledge of its inhabitants. Presently, there is a pressing need to understand physiological mechanisms that led this diversity of cultivated plants and their ancestors to persist and an urgency to implement management practices for its conservation.

Plant physiological research in Mexico is helping to explain questions of interest at various scales, from molecules (Vargas-Soto et al. 2009; Ricalde et al. 2010; de la Rosa-Manzano et al. 2015; Santiago et al. 2017) to whole plant processes (Cervera et al. 2006, 2007; Riaño and Briones 2013; Riaño-Ospina et al. 2015), to communities and ecosystems (Reyes-García 2012; Cach-Pérez et al. 2013; Chilpa-Galván et al. 2013; Méndez-Barroso et al. 2014; Sanaphre-Villanueva et al. 2017), for functional diversity of seeds and its application to restoration (Orozco-Segovia and Sanchez-Coronado 2009).

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